



Impact of warming and reduced precipitation on photosynthetic and remote sensing properties of peatland vegetation

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ABSTRACT

Global warming is an important issue which is leading to considerable changes in biomes. Environmental biologists are continuously assessing how global warming is going to impact the current population. Peatlands are one of the most important component of the terrestrial ecosystems which makes only 3% of them but contain around 40% of soil organic carbon. The composition of peatland vegetation impacts a range of ecosystem functions, therefore, with a change in composition, the behavior and structure of peatland plant communities are predicted to change. This work is focused on the response of Sphagnum peatland (in Poland), to the manipulated environmental conditions. The experimental design consisted of four treatments (control, warming, reduced precipitation, and a combination of warming & reduced precipitation), three replicates of each. Active warming with infrared heaters (~1.0–1.4 °C peat temperature increase) and an automatic curtain to reduce precipitation (~30% reduction in the rain) was applied continuously since 2015. The warming and reduced precipitation caused a significant variation in the vegetation indices such as Normalized Difference Vegetation Index (NDVI), Photochemical Reflectance Index (PRI), Water Band Index (WBI), and Chlorophyll Green Index (CI_{green}) between manipulated sites. The abundance of major plant species was recorded between manipulated sites. The prompt chlorophyll fluorescence measurement was performed in the peak of the vegetation season of August 2017 which had shown a significant variation in photosynthetic induction curve and different photosynthetic parameters from the same plant species in between the manipulated sites. The data clearly indicate that a short-term climate manipulation resulted in the change of plant abundance and its physiology, which varied for different plant species. Our study indicates that the different plant species respond differently to climate change. The study also proposes the significance of simple vegetation indices for peatland vegetation observation.

1. Introduction

The global environment is changing due to several natural and anthropogenic activities, which are causing considerable threat to life on Earth (Hodson, 2017). The impact of climate change on the Earth biomes is complex and difficult to predict, therefore, it is a concern for the global population. Recently, the Paris agreement was signed by 196 countries to distribute the responsibilities in-between, and act to prevent climate change (UNFCCC, 2015). The Paris agreement is meant to keep the global average temperature well below 2 °C above pre-industrial levels (Corlett, 2016). The rise in global temperature even by 2 °C means a significant enhancement in earth surface warming, which

may lead to changes in several climatic parameters including rainfall (Corlett, 2016). Recent studies have shown that climate change may lead to phenological changes in the plants (Ovaskainen et al., 2013; Ge et al., 2015). About 1 °C of global warming was observed to change in the flowering period and a delay of the leaf fall in autumn (Ge et al., 2015). Some of the plant species were observed to extend their flowering zone towards the poles and/or high altitudes (Hijioka et al., 2014). The studies performed on different plant species in various environmental conditions and climate zones indicated an evident change in the plant responses to climate changes. When climate change exceed the natural variation of a plant species, it may results into acclimation (physiological changes in one generation), evolutionally adaptation,

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shifting of species ranges, or the extinction (Corlett, 2016).

Photosynthesis is one of the most important phenomenon in plants, which converts light energy into chemical energy. It is the phenomenon, which is proven to be very sensitive to any environmental changes (Kalaji et al., 2014, 2018). Therefore, by measuring the photosynthetic activity it is possible to assess the physiological status of the plant. There are different ways to estimate non-invasively the photosynthetic process in plants, among them fluorescence-based techniques are most studied and contains detailed step-wise information about photosynthetic processes (Kalaji et al., 2014).

Peatlands store organic matter under waterlogged conditions. The waterlogging creates anoxic conditions, resulting in the low decomposition of plant material, which ultimately results into effective storage of organic carbon (Wieder et al., 2006). Peatland cover only 3% of the terrestrial area but contains around 40% of soil organic carbon (Jungkunst et al., 2012). Some of the recent studies have shown that global warming may cause significant enhancement in carbon loss from peatlands (Bragazza et al., 2016; Samson et al., 2018; Gallego-Sala et al., 2018). In the experiment with an addition of nitrogen and artificial warming of peatland, Peichl et al. (2018) observed a significant variation in maximum gross primary productivity within experimental plots. The authors related the variation in maximum gross primary productivity between plots with the changes in vegetation species composition and phenology rather than abiotic factors (Peichl et al., 2018). Some of the other studies on peatland have also shown that the species composition plays an important role in maintenance of carbon balance for peatland (Strack et al., 2006; Goud et al., 2017). Still there are limitation in information regarding the impact of global warming or climate change on the ecophysiological condition of peatland vegetation. Therefore, in this study the focus was given from canopy to plant level, for the purpose to find how different peatland plant species will behave under warming and reduced precipitation. Remote-sensed spectral vegetative indices were considered to evaluate overall impact of climate manipulation on peatland surface and vegetation, whereas, chlorophyll concentration and fluorescence was considered for the purpose to identify the plant ecophysiological condition. Dry mass was considered to find total carbon assimilation in plants, whereas, differences in plant distribution was observed to check if short term climate manipulation has caused any changes in the structure of peatland vegetation.

Rzeczyn peatland in Poland was selected for this study because of the established climate manipulation setup, which is there since 2014. In this work, the measurements were performed on the plants from treatments which have been manipulated continuously for 3 years by active methods to create conditions which imitate global warming. Our study is the first where the difference in photosynthetic activity was considered for the purpose to identify the impact of climate manipulation on peatland vegetation in active warming conditions.

2. Material and methods

2.1. Site description

WETMAN climate field experiment is located at Rzeczyn poor fen (52°45'43"N 16°18'35"E, 54 m a.s.l.) in western Poland (Fig. 1). The experiment was designed in 2014 within the WETMAN project in order to evaluate the effect of warming and reduced precipitation on carbon fluxes, vegetation, microbes and hydrochemistry (Juszczak et al., 2017; Rastogi et al., 2018). The distinctive feature of the experiment is that it is located on the water-saturated layer of 30–70 cm thick floating *Sphagnum* mat (Juszczak et al., 2013; Acosta et al., 2017). *Sphagnum fallax*, *S. angustifolium* and *S. teres* dominates among bryophytes, while *Carex rostrata*, *C. limosa*, *Eriophorum angustifolium* as well as *Oxycoccus palustris* dominate among vascular plants (Łuców et al. 2017). Below the peat carpet, there is a water gap and thick lake sediment of 9–10 meters (Juszczak and Augustin, 2013; Milecka et al., 2016). In the

middle of the peatland there is a shallow lake. The process of the peatland expansion started 200 years ago (Lamentowicz et al., 2015).

The WETMAN experimental design consists of four treatments replicated three times: control (C); warming (W); reduced precipitation (RP), and combination of warming and reduced precipitation (WRP). The sites are stabilized with the stainless frames installed permanently in the peat surface and consists of the three plots each (Fig. 1). Active methods of manipulations were used in order to increase temperatures (by infrared heaters 400 W × 4 per site) and reduce precipitation (by using automatic retractable curtain, covering the site only during nighttime hours after sensing the rain, and only in the period from March till November) (Juszczak et al., 2017).

The peat temperature was measured continuously by using T-107 thermistors (Campbell Sci. USA) in each of the twelve sites at 2 cm depth, whereas, four heated TPG-124-H24 rain gauges (ASTER, Poland) were installed in the middle of the four sites, to have two sensors exposed to rain-manipulated and two to non-rain-manipulated conditions for the measurement of precipitation.

2.2. Measurement of reflectance and calculation of spectral vegetation indices

Surface reflectance and carbon fluxes were measured continuously at the WETMAN site with automated mobile platform moving in the west-east direction along the site (Juszczak et al., 2017). First reflectance measurements were taken for each plot and then subsequent chamber measurements were taken in order to determine carbon dioxide and methane fluxes (not presented nor discussed in this study). Spectral characteristics of the surface are measured with two pairs of four channels SKR1860 sensors of Skye Instruments Ltd., UK, installed on an arm 50 cm in front of the moving platform and 70 cm above the surface at nadir position. The sensors were calibrated by the manufacturer and the uncertainty of the measured fluxes of radiation was smaller than ± 5%. The footprint of the sensor is around 35 cm in diameter and perfectly fits to the middle of the plots. Sensors are connected to the CR1000 datalogger (Campbell Sci., USA) to record signals with 10 s intervals. The platform stops and reflectance measurements are taken for 2 min above each measuring plot. Incident and reflected radiation was recorded at wavelengths of 531 nm, 550 nm, 570 nm, 670 nm, 850 nm, 900 nm, 970 nm and 1240 nm with the bandwidth of 10 nm. Reflectance (ρ) is calculated as a ratio of reflected to incident radiation for certain band from downwards and upwards facing sensors, respectively. As the measurements for the pair of sensors are taken at the same time any errors resulting from variability in the weather conditions are prevented. Based on the calculated reflectance several vegetation indices (VIs) are computed to reflect greenness of the surface (e.g. Normalized Difference Vegetation Index, *NDVI*), xanthophyll cycle pigments (Photochemical Reflectance Index, *PRI*), chlorophyll content (e.g. Chlorophyll Index Green, *CI_{green}*) and water content in the plants (e.g. Water Band Index, *WBI*) (Table 1). *NDVI*, *PRI*, and *CI_{green}* were considered because of their importance in providing the information regarding vegetation status, whereas, *WBI* was considered, as it indicates the canopy water content. To compute the vegetation indices only the reflectance values measured around the solar noon ± 2 h were filtered from the measured data. Measurements taken till one hour after rain were excluded from the analyses.

2.3. Measurement and calculation of photosynthetic parameters

The month of August was chosen for the photosynthetic parameters measurement because it is considered to be the optimal period for the growth of most of the plants found in the peatland. The measurements were performed on 7th, 8th and 10th of August 2017. Chlorophyll *a* fluorescence measurement was performed on the middle region of mature leaves of vascular plants by using Plant Efficiency Analyzer (Handy PEA fluorometer, Hansatech Instrument Ltd., King's Lynn, Norfolk,

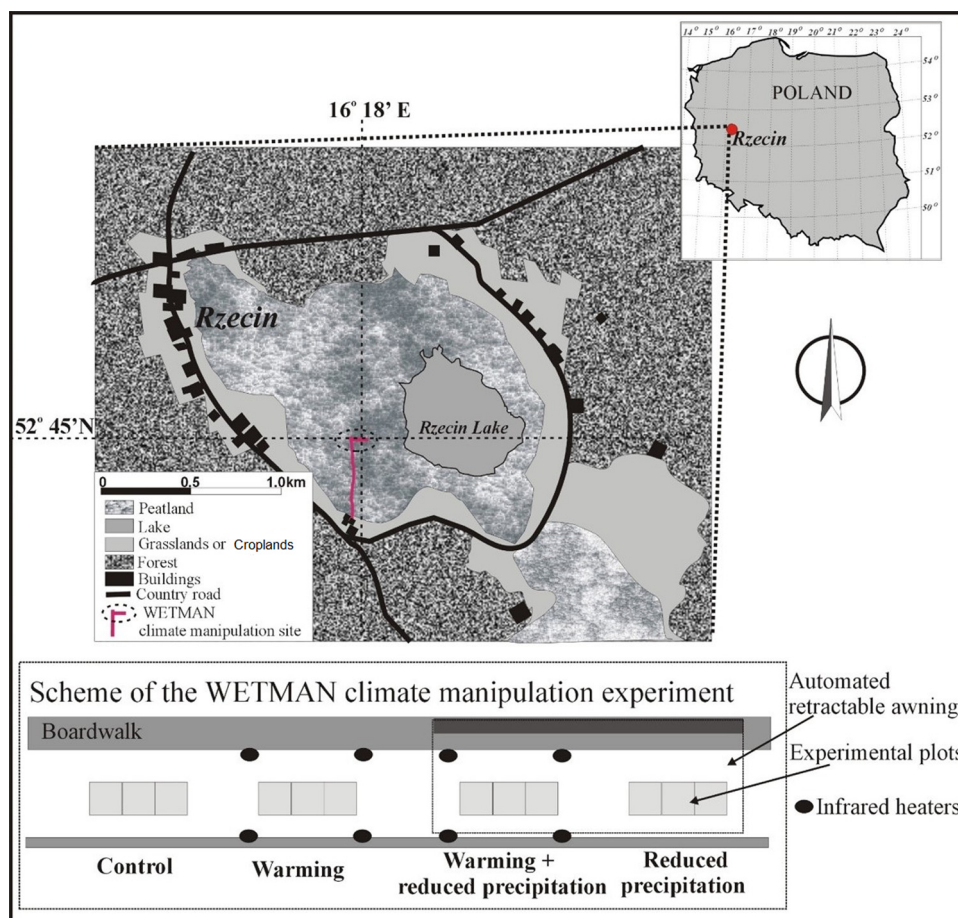


Fig. 1. The location of experimental site in western Poland, and the scheme for the WETMAN climate manipulation experiment, showing four experimental conditions Control, Warming, Warming + Reduced precipitation, and Reduced precipitation.

Table 1

Spectral vegetation indices calculated from ground-based spectroscopy (ρ – reflectance at a given wavelength).

Index	Formula	Reference
NDVI	$NDVI = \frac{\rho_{850} - \rho_{670}}{\rho_{850} + \rho_{670}}$	Rouse et al. (1974)
CI_{green}	$CI_{green} = \frac{\rho_{850}}{\rho_{560}} - 1$	Gitelson et al. (2003)
PRI	$PRI = \frac{\rho_{570} - \rho_{531}}{\rho_{570} + \rho_{531}}$	Gamon et al. (1992)
WBI	$WBI = \frac{\rho_{900}}{\rho_{970}}$	Peñuelas et al. (1993)

England). The head portion of mosses were used for Chlorophyll *a* fluorescence measurement from *Sphagnum*. Before measurements, the plant samples were dark adapted for 45–60 minutes by using leaf clip provided by the producer of *Handy PEA fluorometer*. A detailed analysis of the measured signals of chlorophyll fluorescence was conducted using a JIP test developed in the Laboratory of Bioenergetics of the University of Geneva in Switzerland, using *Biolyzer version 3.0.6 software*, for the purpose to calculate different fluorescence parameters. For statistical relevance three random plants of the same species were measured from a plot. The measurement from 3 different days was compared, and the chlorophyll induction curves (also known as OJIP curve) were drawn from the mean of the obtained data points.

2.4. Measurement and calculation of chlorophyll content

The chlorophyll content was measured noninvasively by using CCM 300 (OPTI-SCIENCES, USA). The measurement was conducted on four

plant species from each of the twelve plots. *Carex rostrata*, *Oxycoccus palustris*, *Sphagnum* and *Menyanthes trifoliata* were selected. Three random plants of the same species from a plot were selected for calculation of average species-related total chlorophyll content ($Ch_{tot-spp.}$), then the plot-specific total chlorophyll content ($Ch_{tot-plot}$) was calculated as an average weighted mean for the plots, taking into account the percentage of plant species abundance. Four plant species considered in this study make around 90–95% of the total vegetation cover of the plot, while for this study the plot was assumed to consist of only these four plant species and multiplied according to plant species concentration to reach 100% contribution of vegetation, for the purpose to calculate $Ch_{tot-plot}$.

2.5. Measurement and calculation of fresh and dry weight

The vascular plants were measured for its fresh and dry weight. The fresh leaves were isolated from the peatland and preserved in a zipped polybag in cold condition for about two hours (time required for coming to lab from the experimental site). Immediately after removing the extra moisture by using blotting paper, the leaves were detached from the stem and fresh weight was measured. For *Carex rostrata* and *Menyanthes trifoliata* one full grown leaf was measured (5 repetitions/plot) whereas, for *Oxycoccus palustris* - 20 leaves from a branch were separated and measured together (5 repetitions/plot). The measured leaves were kept for drying at 39 °C for 48 h and then measured for its dry weight. The dry weight was again measured after 72 h, but no difference was observed in between 48 and 72 h.

2.6. Vegetation measurements

Plant species cover was measured using the digital image analysis (Buttler et al., 2015) in August 2014 and 2017. A wooden frame of 50 x 50 cm was used, which was further divided into four 25 x 25 cm parts. Four high-resolution photographs were captured from one site by using Nikon D300S (Nikon Corporation, Shinagawa, Tokyo, Japan). The photographs were taken manually by hand from approximately 1 m height from ground at nadir position. Plant species were identified at 200% digital magnification in 100 measuring points from one photograph. Because of the complication of separation between *Eriophorum angustifolium* (presence was very rare on sites studied) from the *Carex* spp., these taxa were combined together similarly as *Sphagnum*.

2.7. Statistical analyses

All the data was analyzed according to the experimental design, using Origin (Origin Lab, USA), and Statistica 8.0 (Statsoft Inc., Tulsa, OK, USA). The mean and standard deviation were calculated for each plot and sites and compared with the data obtained from other sites. The mean of each trait was compared to the control according to the Duncan multiple range test at $p \leq 0.05$. One way ANOVA was performed to test the variance between data.

3. Results

3.1. Impact of manipulation on peat temperature and precipitation

An increase in the peat temperature at 2 cm depth was observed in August 2017 for all the manipulated sites, where the average observed temperature was around 17.5 °C for control site and around 18.5 °C for the manipulated sites. The increase in peat temperature in W and RP was around 1 °C above the control (Fig. 2). Whereas in WRP the increase of peat temperature was the highest and exceeded 1.7 °C in relation to the control. The means of the peat temperature observed at manipulated sites were significantly different if compared to the control ($p < 0.01$). Till the end of July 2017 the sum of the precipitation at non-manipulated sites reached 530 mm, while it was reduced by around 38% (till 324 mm) at the rain-manipulated sites.

3.2. Impact of manipulation on spectral vegetation indices

Average values of NDVI and CI_{green} indices for the warm period of 2017 (from May to August) were the highest at the control site and reached around 0.73 ± 0.028 and 3.2 ± 0.42 , respectively. Values of these indices lowered down at the manipulated sites and reached the smallest values at the site exposed for reduced precipitation, indicating

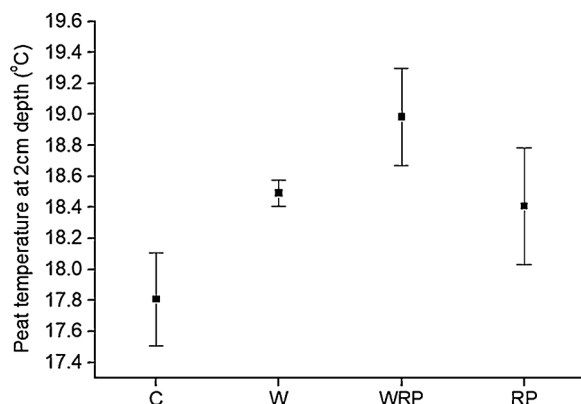


Fig. 2. Impact of manipulation on experimental sites. The graph shows the mean temperature with standard deviation at 2 cm depth for August 2017, the mean was observed to be significant at $P < 0.001$ level.

decrease of surface greenness and reduction of chlorophyll content in the plants exposed for manipulation (Fig. 3). The means for NDVI and CI_{green} were significantly different if compared to the control ($p < 0.05$). PRI was observed to be significantly lower for W ($p = 0.00175$) and WRP ($p = 0.0387$), whereas the difference was insignificant ($p = 0.98$) for RP sites (Fig. 3). WBI shows a slight increase in W, and RP sites (which was statistically insignificant with $p > 0.1$), whereas, a significant ($p = 9.29 \times 10^{-9}$) decrease in WBI was observed in WRP site when compared with C (Fig. 3).

3.3. Impact of manipulation on transient fluorescence curve (OJIP curve) and photosynthetic parameters

Transient fluorescence curve for the four important peatland vegetation was analyzed from each manipulated site in the peak of the growing season in August 2017. For comparison purpose, a single normalized curve against the control was plotted as the ratio of relative fluorescence at time t (F_t) to relative fluorescence at time 0 (F_0). Each of the steps (O, J, I, and P) are associated with different processes of light reactions in photosynthesis (Kalaji et al., 2017). The transient fluorescence curve for *Carex rostrata* at the manipulated sites was significantly different at J, I and P steps, with very prominent differences in W and WRP sites (Fig. 4A). In *Oxycoccus palustris* the impact of climate manipulation on different steps of OJIP curve was more prominent for RP and WRP sites (Fig. 4B). The OJIP curve for *Sphagnum* was very different in between control and manipulated sites (Fig. 4C). The plants from W and WRP have shown the lowest values for J, I, and P steps whereas, the plants from RP site have shown the intermediate values of J, I, and P for *Sphagnum* whereas, *Menyanthes trifoliata* was observed to show the lowest values for point J, I, and P in W and WRP sites (Fig. 4D).

Different photosynthetic parameters from the plants at different manipulated sites have indicated a clear difference in different photochemical processes (Fig. 5). The ratio of photochemical to non-photochemical quantum efficiencies (F_v/F_0) was observed to be decreased for the manipulated sites except W for *Oxycoccus palustris*. The impact of manipulation on F_v/F_0 was much intense for *Sphagnum* in W and WRP sites (Fig. 5A). Absorption flux per one active reaction center (ABS/RC) was observed to be increased for the plants of manipulated sites, with the exception of *Carex rostrata* (Fig. 5B). The maximum quantum yield of primary photochemical reactions at time 0 (Φ_{P0}) was observed to be decreased for the plants from manipulated sites except for *Oxycoccus palustris* from W sites (Fig. 5C), but interestingly a significant ($p = 0.006$) increase in quantum yield of electron transport at time 0 (Φ_{E0}) was observed for *Sphagnum*. The value of Φ_{E0} for *Menyanthes trifoliata* was observed to be very high (mean = 0.88) in comparison to other plants in C sites (mean < 0.38) (Fig. 5D). The probability of an electron trapped by PSII to reach the electron transport chain outside Q_A^- (ψ_0) was observed to vary in different plants from different manipulated sites (Fig. 5E). A significant ($p = 0.48 \times 10^{-4}$) increase in ψ_0 was observed from RP site for *Sphagnum*, whereas a significant decrease from W ($p = 0.0016$) and WRP ($p = 0.0034$) sites was observed for *Menyanthes trifoliata* (Fig. 5E). The PS II performance index ($PI(ABS)$) was observed to be significantly decreased for W and WRP sites for *Carex rostrata*, *Sphagnum*, and *Menyanthes trifoliata*, whereas, *Oxycoccus palustris* have shown a slight increase in $PI(ABS)$ from the plant at W site and a decrease from the plants of RP site, an intermediate response was observed for the *Oxycoccus palustris* in WRP site (Fig. 5F). *Sphagnum* has shown an increase in RP site for $PI(ABS)$ value.

3.3.1. Impact of manipulation on chlorophyll content of vascular plants

A significant decrease in chlorophyll content was observed in WRP and RP sites in *Carex rostrata* and *Sphagnum*, whereas, interestingly an increase in chlorophyll content was observed in *Menyanthes trifoliata* (Fig. 6). In W site *Oxycoccus palustris* was observed to have the highest chlorophyll content. The calculated $Ch_{tot-site}$ was compared with CI_{green}

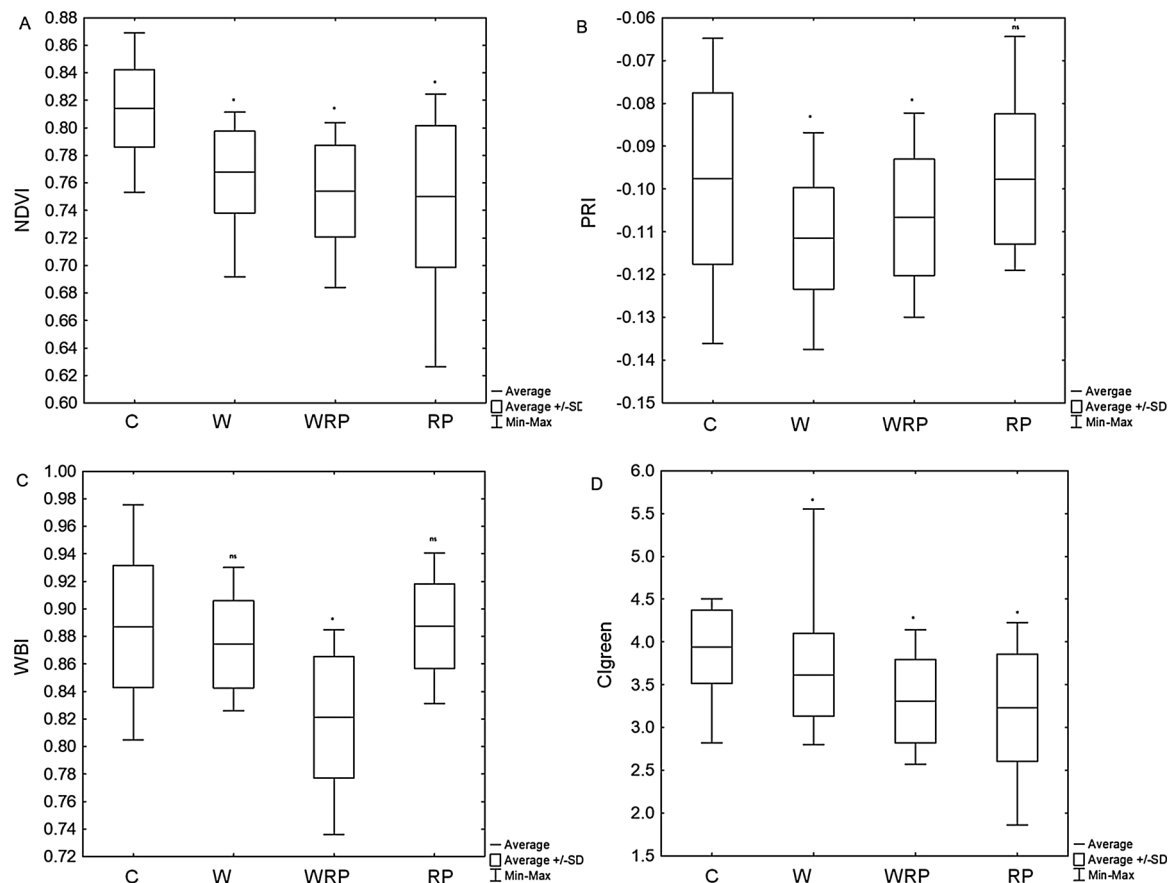


Fig. 3. Effect of climate manipulation on different spectral vegetation indices where “A” is showing Normalized Difference Vegetation Index (NDVI), “B” represents Photochemical Reflectance Index (PRI) “C” is Water Band Index (WBI), and “D” is Chlorophyll Green Index (CI_{green}). The box plot is drawn for mean with standard deviation, and contain the maximum and minimum values of indices. The mean was observed to be significant at $p < 0.05$ level.

– index developed for the purpose of remote-based estimation of chlorophyll content in plants, for the purpose to verify hypothesis that CI_{green} can be applied for remote estimation of chlorophyll content in peatland canopies. We found good agreement ($R^2 = 0.77$) between these datasets, although variation of CI_{green} signal was much higher than for values measured with CCM-300 chlorophyllometer (Fig. 7).

3.3.2. Impact of manipulation on fresh and dry weight

An increase in fresh and dry weight was observed in *Menyanthes trifoliata* in W and WRP sites (Fig. 8), whereas fresh weight was observed to be decreased in W and WRP sites for *Carex* spp., No significant difference was observed in dry weight for *Carex* spp. and *Oxycoccus palustris* when compared between the different sites.

3.3.3. Impact of manipulation on plant distribution

The differences in between mosses and vascular plants percentage contribution among C and manipulated sites was observed to be statistically insignificant for the year 2017 (Fig. 9A). For the purpose to analyze the vascular plants contribution in more details, they were divided into two groups one consisted of *Oxycoccus palustris* whereas, other consisted of *Carex* spp. and *Eriophorum angustifolium*. The abundance of *Carex* spp. and *Eriophorum angustifolium* in W and WRP sites were observed to be higher in 2017 than in 2014 respectively. The percentage contribution of *Oxycoccus palustris* was higher for the year 2017 when compared with 2014, but for the year 2017, % contribution was observed to be slightly lower in manipulated sites when compared with C (Fig. 9B).

4. Discussion

Peatlands are a relevant carbon sink, which store almost one third of terrestrial carbon, thus any changes in air temperature and peat degradation may play an important role in enhancing global warming, due to its potential to become a carbon source (Dieleman et al., 2016; Gout et al. 2017). The elevation in temperature or lower ground water levels may cause a significant negative impact on peatlands (Bragazza et al., 2013; Malhotra et al., 2016). Observation of various different vegetation indices is very popular and efficient method to detect the impact of climate change at the ecosystem level, but it has its limitations and it is hard to say anything about the plant physiology by this method, especially when the ecosystem is diverse and composed of different plant communities (Glenn et al., 2008; Kalacska et al., 2015). Therefore, along with remote sensing indices, this study also considered few other properties of peatland vegetation, such as chlorophyll concentration, fresh and dry weight, and photosynthetic efficiency of plant species in the peatland area, for the purpose to identify the impact of climate manipulation on the peatland vegetation at the plant level.

The results indicated that NDVI was significantly influenced by RP when compared with W (Fig. 3). A decrease in NDVI indicates a decrease in the surface greenness, which may also indicate a decrease in chlorophyll concentration (Tucker et al., 1985). As the greenness is dependent on chlorophyll concentration, a significant decrease in chlorophyll concentration of the two dominating taxa (*Carex* spp. and *Sphagnum*) indicates that low chlorophyll concentration in dominating species is the reason for lower NDVI in RP sites.

The PRI is considered to be a good indicator for the functionality of photosynthetic apparatus (Garbulsky et al., 2011; Gamon et al., 1992). Generally, PRI is used to study the changes in xanthophyll cycle activity

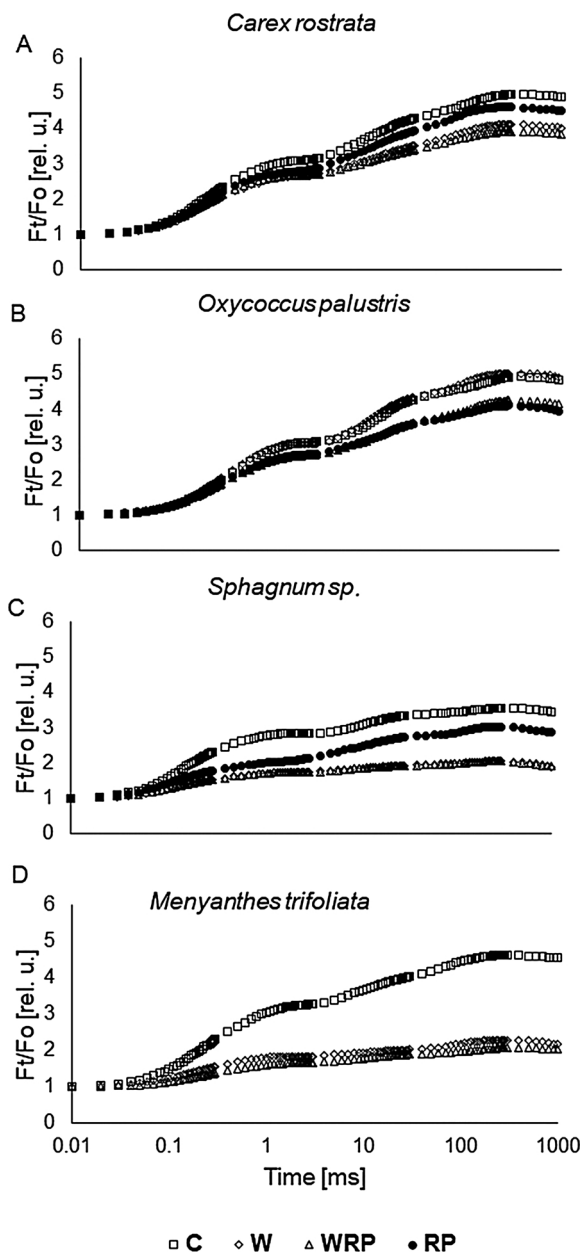


Fig. 4. Effect of climate manipulation on fluorescence induction curves for peatland vegetation. It represents the transient chlorophyll *a* fluorescence induction curves for different studied conditions (Control, C; Warming, W; Warming + Reduced precipitation, WRP; and Reduced precipitation, RP) for selected plants “A” *Carex rostrata*, “B” *Oxycoccus palustris*, “C” *Sphagnum*, and “D” *Menyanthes trifoliata*.

at a short-term scale (from hours to days), but also it is used to estimate the changes in the pigment ratio at long-term scale (weeks to months) (Peñuelas et al., 1995; Gamon and Berry, 2012; Wong and Gamon, 2015; Zhang et al., 2017). As our study was a long term study, *PRI* behaved like an index for photosynthetic regulation and illustrated the activation/deactivation of photo-protective carotenoid pigments for the purpose to regulate photosynthetic activity in response to environmental changes. The changes in Carotenoids/Chlorophyll (Car/Chl) ratios plays a key role in photosynthetic regulation and is associated with variability in *PRI* (Porcar-Castell et al., 2012). Therefore, a decrease in *PRI* indirectly suggested that changes in Car/Chl had a significant effect on photosynthetic down-regulation in W and WRP sites.

Further a comparison of *PI(abs)* was done with *PRI* and *NDVI* for the purpose to find close correlation of these VIs with PSII performance,

thus photosynthetic activity (Fig. 10). The *mehPI(abs)* from three major species (except *Menyanthes trifoliata*, due to its less than 1% proportion) was compared with *NDVI* and *PRI* from all sites to find that *PRI* shows good correlation with *PI(abs)* for *Sphagnum* and *Carex rostrata* but not for *Oxycoccus palustris*, where *NDVI* does not show correlation with *PI(abs)*. The reason may be the insensitivity of *Oxycoccus palustris* to warming (clearly seen by different results of fresh and dry weight, chlorophyll concentration or fluorescence data), which covers around 40% area of different sites, whereas *Carex* and *Sphagnum* cover around 60% of sites (Fig. 9). The results clearly indicate the reliability of *PRI* for the purpose to detect photosynthetic activity in *Sphagnum* and *Carex* spp. dominated peatland. The other VIs considered in this study were *WBI* and *CI_{green}*. Due to reduced precipitation and enhanced evapotranspiration, *WBI* was observed to be the lowest for WRP site, which may indicate lower canopy water content in the peatland vegetation (Peñuelas et al., 1993). *CI_{green}* represents the chlorophyll concentration in the sites (Hatfield and Prueger, 2010). A good correlation ($r^2 = 0.766$) between *CI_{green}* and chlorophyll content at leaf level validate the significance of *CI_{green}*, and presents this index as a good remote sensing proxy of chlorophyll content for peatland vegetation.

In the last decade the JIP test has established itself as a standard method to quickly estimate the plant health condition (Bussotti et al., 2007, 2011; Rapacz et al., 2015; Kalaji et al., 2018; Rastogi et al., 2019). The overall decrease in fluorescence induction curve shows that the manipulation caused an overall decrease in photosynthetic response, except in the case of *Oxycoccus palustris* where only warming of the site does not influence the curve. The obtained data indicated that the warming of the site was not an influencing factor for *Oxycoccus palustris*, whereas, it was an influencing factor for the other studied plant species, in regards to photosynthetic activity. The photosynthetic induction curve for *Sphagnum* was quite low even for C sites when compared with other plant, which indicated that warmness of August was already a factor which was negatively influencing the bryophytes. When compared between manipulated sites, the RP site was observed to be less effective in causing the deviation of the fluorescence induction curve for *Sphagnum* and *Carex rostrata* whereas, for *Oxycoccus palustris* it was the most influencing factor when compared with W and WRP sites. The observation clearly indicates that warming was not an influencing or a positive factor for *Oxycoccus palustris*. However, for other plant species warming was observed to deviate the photosynthetic activity thus acted as a stress factor.

Due to the damage or maturity of photosynthetic apparatus the maximum efficiency of water diffusion reaction (F_v/F_o) was observed to be low in manipulated sites except for *Oxycoccus palustris* in W site. The damage or maturity of photosynthetic apparatus can be also estimated by the presence of significantly higher level of active reaction centers (RCs) in manipulated sites for *Sphagnum* and *Menyanthes trifoliata*, which was observed in the form of higher ABS/RC . The probability of energy from absorbed photons to be trapped by PSII RCs under manipulated conditions was observed to be less in manipulated sites except for *Oxycoccus palustris* in W, shown by a decrease in ϕ_{P_0} . The observation is in agreement with previous reports, where high temperature stress was observed to cause a decline in ϕ_{P_0} value (Mathur and Jajoo, 2014). The increase in Ψ_0 was observed in RP sites for *Sphagnum* and *Carex rostrata* indicated the probability of RC trapped exciton to move beyond Quinone A^- (Q_A^-) was high, which can be also seen by increased ϕ_{E_0} , indicating higher quantum yield of electron transport at time 0 ($t = 0$). The observation indicated that, the presence of lower amount of active reaction center was working efficiently to makeup the plants need, and shows that the plants were trying to adapt to RP condition, which can be observed by a higher value of *PI(abs)*. The observation also indicated that the RP was comparatively less affecting the photosynthetic apparatus for *Sphagnum* and *Carex rostrata* in respect to W and WRP sites. Thus, from the observation it is clear that the warming is a crucial factor for *Carex rostrata* and *Sphagnum* in comparison to RP. Whereas, the reduction of precipitation seems to be

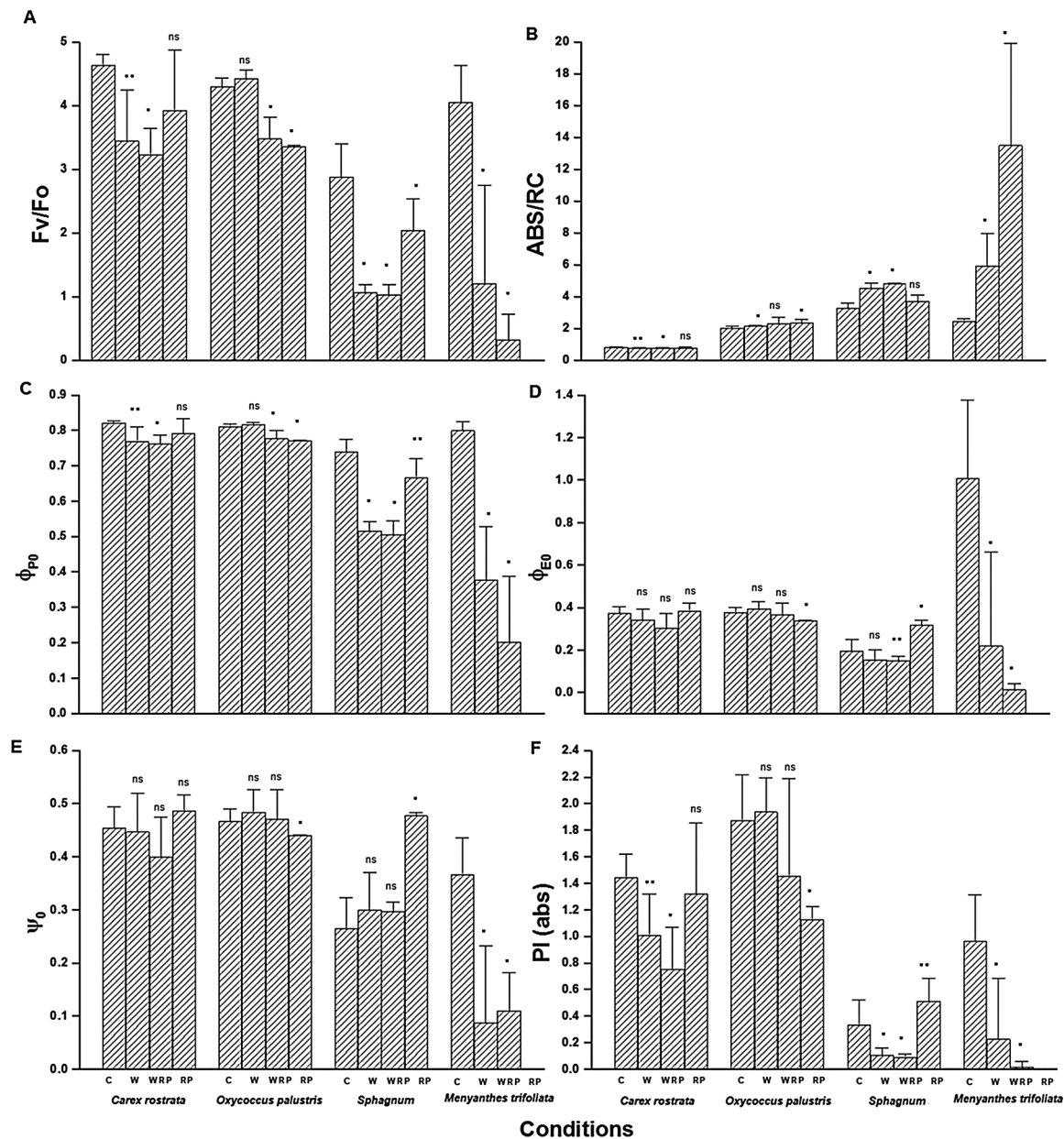


Fig. 5. Effect of climate manipulation on different photosynthetic parameters of different plants. Where mean and standard deviation of photosynthetic factors F_v/F_0 (the ratio of photochemical to non-photochemical quantum efficiencies) “A”, ABS/RC (absorption flux per one active reaction center) “B”, Φ_{P0} (the maximum quantum yield of primary photochemical reactions at time 0) “C”, Φ_{E0} (quantum yield of electron transport at time 0) “D”, Ψ_0 (the probability of an electron trapped by PSII to reach the electron transport chain outside Q_A^-) “E”, and $PI(abs)$ (PS II performance index) “F” under different manipulated condition (Control, C; Warming, W; Warming + Reduced precipitation, WRP; and Reduced precipitation, RP) for different plant species. *Menyanthes trifoliata* was absent in reduced precipitation (RP) sites.

more crucial for *Oxycoccus palustris*, where W shows neutral/positive influence on plant. However, when warming is combined with reduced precipitation (WRP site) the photosynthetic apparatus for *Oxycoccus palustris* seems to work more like at RP site. The significant difference in photosynthetic properties of *Menyanthes trifoliata* can be contributed to its sensitivity to temperature and longer growing season, as the plants in manipulated sites were more mature than the plants at control sites, which could be observed by higher fresh and dry weight of leaves (Fig. 8). The observation of plant chlorophyll content also confirmed the observation with the higher amount of chlorophyll in *Menyanthes trifoliata* (Fig. 6), even if the photosynthetic activity was observed to be less (Fig. 5). The plant distribution data indicated a slight decrease in total vascular plants in RP site in comparison to others in the year 2017 (Fig. 9). When compared with the plant distribution before

manipulation of the sites (i.e. August 2014), a significant difference in plants distribution was observed. When the plants were separated for *Carex* spp. and *Oxycoccus palustris*, a clear increase in *Carex* spp. was observed in WRP site, whereas, *Oxycoccus palustris* was observed to be slightly decreased in WRP and RP sites. Simultaneously, the decreases in photosynthetic activity in *Carex rostrata* with an increase in its abundance can be due to earlier beginning of growing season and a longer growing period due to climate manipulation, or the contribution of other grass species which were not considered for chlorophyll content measurement, whereas, considered with *Carex rostrata* in abundance study.

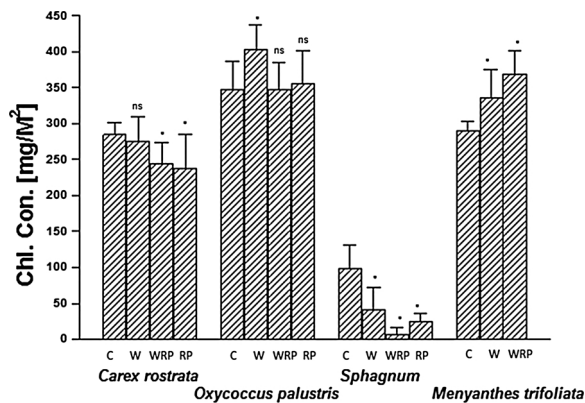


Fig. 6. Effect of climate manipulation on total chlorophyll concentration. X axis shows different plants species under different climate manipulation (Control, C; Warming, W; Warming + Reduced precipitation, WRP; and Reduced precipitation, RP) condition, whereas Y axis indicates total chlorophyll concentration in mg/m^2 . The mean of chlorophyll concentration is plotted with standard deviation, “*” indicates the mean was significant at $p < 0.05$ level, whereas “**” indicates mean in insignificant with $p < 0.1$.

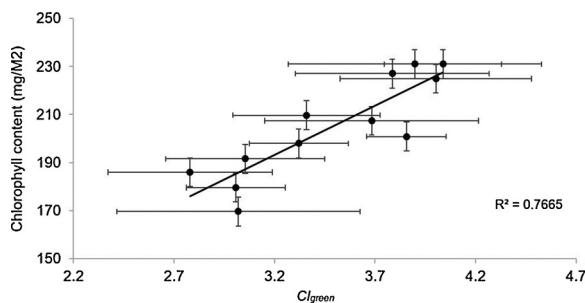


Fig. 7. Relationship between Cl_{green} and chlorophyll content measured at leaf level. Standard deviation is drawn for both the axis and R^2 indicates the correlation between parameters.

5. Conclusion

From this study, it is evident that warming may cause a shift in vegetation structure of the Rzecin peatland. The study also underlines the use of remote sensing indices such as PRI , which was observed to be suitable for the estimation of photosynthetic status of peatland vegetation, but it would fail when the dominant species would be *Oxycoccus*

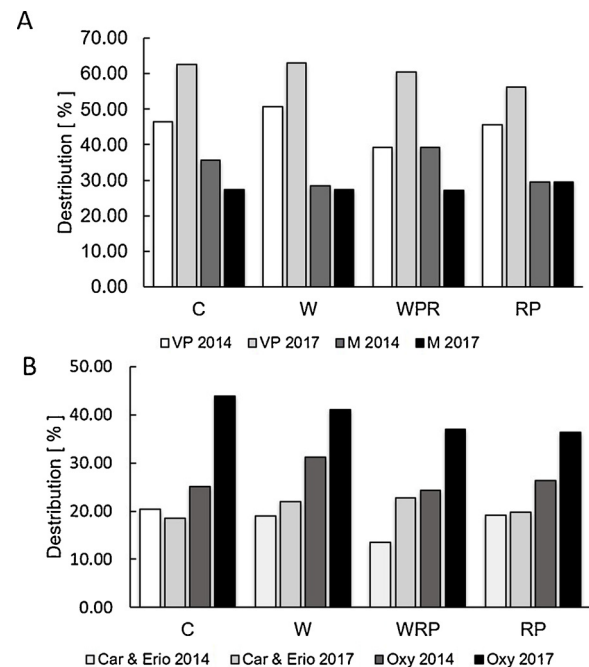


Fig. 9. Effect of climate manipulation on plant distribution. “A” shows the % of vascular plants (VP) and mosses (M) distributed in different climate manipulated sites (Control, C; Warming, W; Warming + Reduced precipitation, WRP; and Reduced precipitation, RP) in two years 2014 (i.e. before the climate manipulation starts) and 2017 (i.e. the year of observation), whereas “B” indicates the % distribution of *Carex* spp. and *Eriophorum angustifolium* (Car & Erio) and *Oxycoccus palustris* (Oxy) for 2014 and 2017.

palustris. The vegetative index Cl_{green} was observed to be useful for the purpose to estimate the total chlorophyll concentration of peatland vegetation. In this study the warming was observed to be not an influencing factor for *Oxycoccus palustris* but was the important factor for *Carex* spp. and *Sphagnum*. A shift in the growing period of vascular plants may impact several environmental factors such as water availability for plants, insects for pollination etc., which may further impact the plant sustainability. The study is important, as it shows how some of the important plant species in peatland may behave in future climatic condition and may cause a change in peatland vegetation. The change in vegetation ultimately may result into interference with stored carbon in peatland, which is a concern at global scale. This work is also

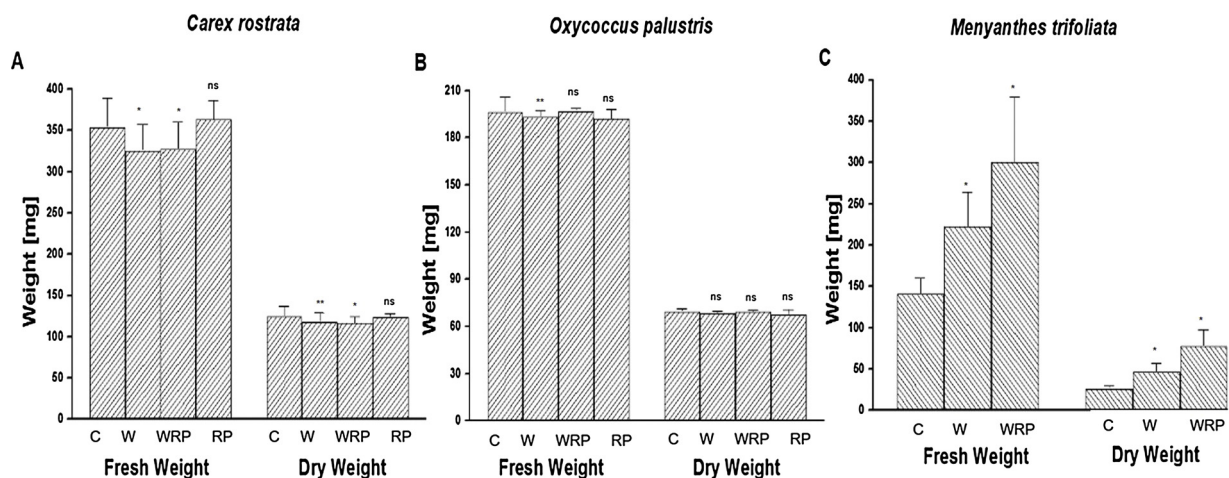


Fig. 8. Effect of climate manipulation on fresh and dry weight of vascular plants under different climate manipulation conditions (Control, C; Warming, W; Warming + Reduced precipitation, WRP; and Reduced precipitation, RP). The average weighted mean is plotted with standard deviations. “*” indicates the mean was significant at $p < 0.05$ level, whereas “**” indicates mean in insignificant with $p < 0.1$.

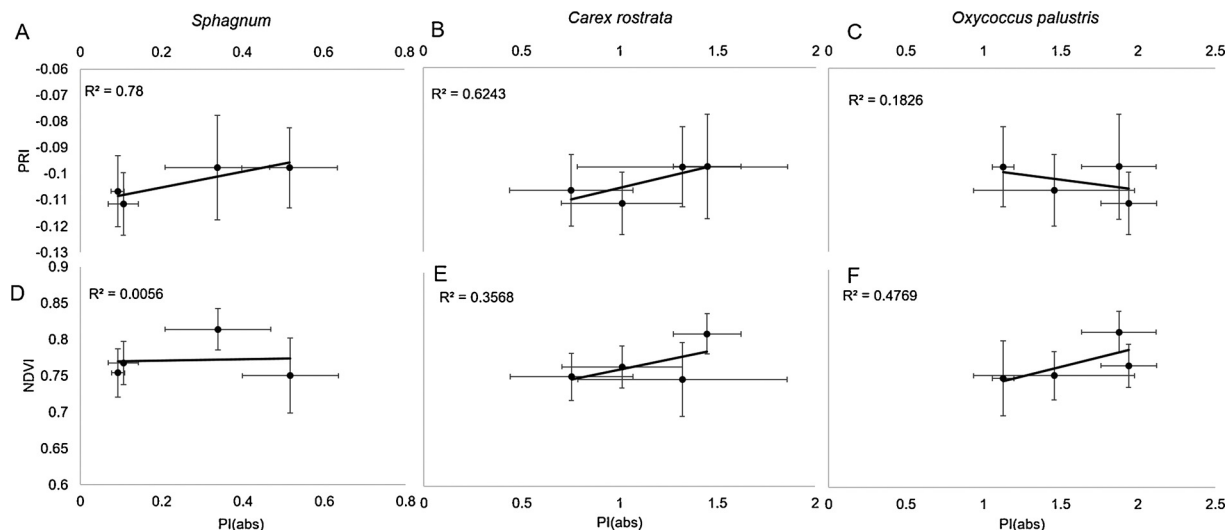


Fig. 10. Relationship of PS II performance index [PI(abs)] with Photochemical Reflectance Index (PRI) “A–C” and Normalized Difference Vegetation Index (NDVI) “D–F” is presented for three major plant species, where vegetative indices were considered for the site whereas photosynthetic parameter was for different plant species. Standard deviation is drawn for both the axis and R^2 indicates the correlation between parameters.

important as it shows that the simple remote sensing indices can be used for the assessment of the chlorophyll content and photosynthesis of peatland vegetation.

Author statement

It is certified that all authors have seen and approved the final version of the revised manuscript titled “Impact of warming and reduced precipitation on photosynthetic and remote sensing properties of peatland vegetation”. We also confirm that the article is the authors' original work, hasn't received prior publication and isn't under consideration for publication elsewhere.

The authors also declare that there is no conflict of interest.

The authors also declare that all the received funding source are properly mentioned in acknowledgement section of the manuscript.

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